MODELING DOLPHIN HABITAT PREFERENCES IN

A SEMI-ENCLOSED BASIN IN GREECE

A Thesis

by

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Submitted to the Office of Graduate and Professional Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

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May 2016

Major Subject: Marine Biology

ABSTRACT

Information on the distribution and habitat preferences of a species or population can be used to assess its status and identify appropriate management action. This is particularly relevant in areas exposed to high human impact, such as the coastal and inland waters of the Mediterranean Sea. The Gulf of Corinth is a 2,400 km^2 semi-enclosed embayment in central Greece, characterized by waters up to 900 m deep. This study focuses on the two most abundant odontocete species occurring in the Gulf: striped dolphins *Stenella coeruleoalba* and common bottlenose dolphins *Tursiops truncatus*. Boat surveys totaling 21,435 km were conducted between 2011 and 2015, yielding 1,873 km of group follows for striped dolphins and 336 km for bottlenose dolphins. Dolphin distribution was investigated by incorporating multiple geographic, bathymetric, environmental and anthropogenic variables in generalized additive models (GAMs) and generalized estimation equations (GEEs). Explanatory variables considered in the modeling process included intensity of survey effort, sea state, sea surface temperature, chlorophyll-*a*, distance to upwelling areas, distance to coast, bottom depth, bottom slope, and distance to sources of human influence (including 17 fish farms, and two large underwater deposits resulting from dumping of industrial byproducts of aluminum production). A total of 68,913 data points were related to these explanatory variables within a geographic information system (GIS). Striped and bottlenose dolphins were never observed together and their tracked movements suggest habitat segregation. Distribution modeling indicated that striped dolphins occur in the central and southern portions of the basin, in waters more than 300 m deep, and with low Chl-*a* concentrations. Bottlenose dolphins use waters less than 300 m deep in the northern sector of the Gulf, with increased occurrence near fish farms. Modeling results indicated no avoidance of industrial dumping areas for either species. Mediterranean subpopulations of striped and

bottlenose dolphins are classified as Vulnerable in the IUCN Red List and the Gulf of Corinth is regarded as a Mediterranean area of high conservation importance for cetaceans. To date, however, management action has been hampered by poor information on cetacean status and habitat use. This thesis contributes baseline data to support ongoing marine spatial planning efforts and support future conservation action, taking into account cetacean habitat needs.

DEDICATION

This thesis is dedicated to my parents and to my-Gio for their extraordinary support and love. Without them, I would never have achieved this goal in my life.

ACKNOWLEDGEMENTS

I would like to acknowledge several people who, in one way or another, greatly influenced the realization of this thesis.

Thanks to my committee chair, Dr. Bernd Würsig, for the chance you gave me to participate in the Marine Biology Interdisciplinary Graduate Program, for all your contagious enthusiasm, for approving all my decisions and for your amazing confidence in my abilities.

Thanks to my committee members Dr. Jane Packard and Dr. William Heyman, for your valuable comments and suggestions during the writing of this thesis.

I also wish to thank Holly Richards, who patiently answered to my never-ending emails, and helped me during all these years. Thank you Christina Irons for your prompt actions in facilitating my travels and for your patience with my last-minute requests. Thank you Bill Elizondo, always being ready to solve my technical computer issues with a smile and in a very 'simpatico' way.

Thanks to my friends and colleagues in Galveston. Thank you Mel and Bernd (again), for supporting me in all possible ways, for being wise friends and being amazingly helpful during my Texas experience. Thank you Sarah, for your always-available hugs and supportive words, no matter how many thousands of miles were between us. Thank you Maelle, your contagious laugh and positive attitude were fundamentally important. Thank you Kristen, my genius friend who rescued me several times from statistic nightmares. Thank you Dara, for inspiring me on how a PhD student should be and behave. Thank you Mithriel, Mari and Greg for always providing precious advice and support.

I have tremendous appreciation for Nathan, who patiently guided and assist me into the world of modeling, always ready to answer my embarrassing statistical questions professionally and modestly; it has been my good fortune to meet you in Galveston.

I'd like to make a special acknowledgment to all my fantastic long-term field collaborators (a team of only girls!). Thank you Nina for all your help with the hard work we've done together in the last five years, from dorsal fins to garden rocks, from mark-recapture matrixes to camel spiders. Than you Dagmar, my lovely German friend, for appreciating my "Greek universe", for sharing photographic moments and for always being positive even when the life-jackets were left at home. Thank you Mariana, for being such a multi-tasking, never-complaining helper, always ready with a smile and positive attitude, even with tons of cutlery to be washed! Thank you Lavinia for your patience, hard work and for always being ready to hold an umbrella during stormy dolphin surveys.

I am grateful to all my other amazing collaborators who worked very hard both in the field and in the office; many thanks to Philippa, Riccardo, Manon, Catarina, Valeria and Eva.

I would like to acknowledge my Greek friends, without whom all the work in Greece would have been incredibly difficult. Thank you Chrisoula and Kostas, for being my "Greek family" and for helping to solve any problem that came up. Thank you Alexis and Vasilis for taking good care of my boat, for always giving priority to my needs and for treating me as a peer. Thank you Christos, for your uniquely friendly support in all the achievements of this project. Thank you Vasilis Valavanis (Hellenic Centre for Marine Research) for providing essential data and information for many areas in Greece. Thank you Margarita Iatrou, for your invaluable work and providing information essential to this study. Thanks to all the fishers who shared their experience with me and taught me what they know about the Gulf of Corinth.

The research for this thesis was conducted in collaboration with OceanCare, which has financially supported my research for many years. Special thanks to my friends Sigi, Silvia, Vera and Fabienne. This project would not have been possible without your constant help. Thank you so much OceanCare!

Thanks to Andrea Sacchi, for your friendship, for sharing a deep love for nature, for your moral and financial support.

Thanks to all my dear friends. Eli, you are more than a sister, a unique and lovely soul, always by my side over many years. Thank you Lux, my “reference friend”, always ready to provide wise and warm support without judgment. Thank you Micki, for being a precious link with my family, being able to justify and see things in a complex and genuine eye.

A heartfelt thanks to my family. Thank you Pichi and Pone, for being my secret angels. Thank you Gil and Giuseppe, for treating me like a daughter, for supporting me in whatever I do and for completing my family circle. Thank you lovely Madda, your sister-like friendship represents an invaluable gift in my life; thank you for being always available and supportive no matter the kind or extent of my “black-clouds”.

My deepest and super-special THANKS go to my treasure, my source of knowledge and inspiration, my soul-enricher, my life-supporter, my beacon in the dark… my-Gio. All this would not have been possible without you.

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INTRODUCTION

Studies of cetacean distribution and identification of the forces that influence habitat choice are critical to understanding cetacean status, and can help elucidate possible anthropogenic impacts (Cañadas et al. 2005). Cetaceans are challenging research subjects because they spend much time underwater in ever-shifting sea state and weather conditions, and are therefore difficult to detect, observe, and follow over long periods of time. As a result of these difficulties, as well as the high economic and logistical burden of field studies, information on cetacean distribution, movements and habitat preferences is often lacking, even in areas as intensively used by humans as the coastal and inland waters of the Mediterranean Sea.

Analyses based on large sets of field data can help relate the observed distribution of cetaceans to environmental and other variables. Several Mediterranean studies have investigated the relationship between cetacean distribution and physiographic or oceanographic features (Cañadas et al. 2005; Cañadas and Hammond 2006; Azzellino et al. 2008; Panigada et al. 2008; Pirotta et al. 2011). These studies have applied spatial analysis and geographic information system (GIS) technology to describe and model species-habitat relationships, investigate variability, and identify critical habitat; but few studies so far have also considered anthropogenic pressures in the modeling process, as done e.g. by Fortuna (2006) and Bonizzoni et al. (2014).

The common bottlenose dolphin *Tursiops truncatus*—hereafter bottlenose dolphin—is the most intensively studied cetacean in the Mediterranean Sea, a region where the species is regularly observed in continental shelf waters (Bearzi et al. 2008c). The Mediterranean subpopulation has been classified as Vulnerable in the IUCN Red List of Threatened Species (Bearzi et al. 2012), a classification based on population decline due to historical culling campaigns and, more recently, to incidental mortality in fishing gears, overfishing of dolphin prey, and habitat degradation (Bearzi et al. 2008c). Several Mediterranean studies indicated that bottlenose dolphin distribution is significantly influenced by bottom depth. In the Ligurian Sea, bottlenose dolphins are mostly confined to the continental shelf, with few sightings beyond the 200 m isobath (Azzellino et al. 2008; Gnone et al. 2011). In the Alboran Sea, bottlenose dolphins occur in areas 200–400 m deep, whereas waters over 600 m are avoided (Cañadas et al. 2002). Bottlenose dolphins around Filicudi Island, Italy, mostly occur in waters between 100 and 300 m (Blasi and Boitani 2012), whereas in the generally shallow northern Adriatic Sea occurrence peaks in waters about 50 m deep (Fortuna 2006). In some cases, bottlenose dolphin distribution seems to be positively influenced by steep bottom profiles (Cañadas et al. 2002; Blasi and Boitani 2012). Apart from bottom depth and contour, bottlenose dolphin distribution was found to be positively influenced by operating bottom trawlers, often followed by the animals in the northern Adriatic Sea (Bearzi et al. 1999; Fortuna 2006), whereas in the Alboran Sea occurrence was higher in areas exploited by local fishers (Cañadas et al. 2002). In the Northern Evoikos Gulf, Greece, bottlenose dolphin occurrence was remarkably higher within 5 km of coastal fish farms, particularly in areas where the farms were tightly clustered (Bonizzoni et al. 2014). Direct disturbance (e.g. from boaters) and underwater noise can negatively affect occurrence of bottlenose dolphins based on studies conducted in non-Mediterraenan areas (Lusseau 2003; Bejder et al. 2006). Similarly negative impacts have been suggested for bottlenose dolphins in the Ligurian Sea (Gnone et al. 2011) and in the northern Adriatic Sea (Fortuna 2006).

The striped dolphin *Stenella coeruleoalba* is the most abundant cetacean in the Mediterranean Sea, where the species is typically found in pelagic waters (Notarbartolo di Sciara et al. 1993; Forcada et al. 1994; Aguilar 2000; Gannier 2005). The Mediterranean subpopulation has been classified as Vulnerable in the IUCN Red List (Aguilar and Gaspari 2012). Main anthropogenic threats thought to have resulted in population decline include contamination by xenobiotic contaminants, overfishing of striped dolphin prey, and mortality in fishing gear, particularly pelagic driftnets (Aguilar and Borrell 1994; Aguilar 2000; Aguilar and Gaspari 2012). Between 1990 and 1992, and between 2006 and 2007, morbillivirus epizootics have had devastating effects on Mediterranean striped dolphins, especially in the western sector where thousands of animals died (Domingo et al. 1990; Aguilar and Raga 1993; Raga et al. 2008). Striped dolphin occurrence in the Mediterranean is strongly related to bathymetry. In the Alboran Sea, occurrence increases at increasing depths and is higher in waters deeper than 600 m, whereas observations in continental shelf waters are rare (Cañadas et al. 2002). Alboran Sea striped dolphins seem to prefer relatively steep bottoms (slope over 20 m km^{-1}). Conversely, striped dolphins in the Ligurian Sea tend to occur in deep waters with a flat bottom contour (Panigada et al. 2008). In this area, occasional observations of striped dolphins near the coast were related to zooplankton accumulation caused by wind-induced currents (Azzellino et al. 2008). Variability in striped dolphin distribution was linked to changes in surface currents, wind strength and direction, and sea surface temperature (Azzellino et al. 2008). Additionally, Panigada et al. (2008) reported a general preference for water temperatures of 21–24°C, as well as an unclear but possibly relevant effects of Chl-*a* concentration.

The seas around Greece host a rich cetacean fauna, bottlenose and striped dolphins being regular in these waters (Frantzis et al. 2003; Frantzis 2009). Cetacean research in Greece started in the 1990s and still relatively little is known about the distribution, abundance and status of dolphins. The most detailed information on bottlenose dolphins comes from a few coastal areas and semi-enclosed bays, such as the Amvrakikos Gulf (Bearzi et al. 2008a), the Inner Ionian Sea Archipelago (Bearzi et al. 2005, 2010), and the Northern Evoikos Gulf (Bonizzoni et al. 2014), with limited information regarding bottlenose dolphin movements (Bearzi et al. 2011b) and interactions with fisheries (Gonzalvo et al. 2010; Piroddi et al. 2010). Some of the bottlenose dolphins photo-identified in the Gulf of Corinth were observed in distant areas outside of the Gulf (up to 265 km apart; Bearzi et al. 2011b).

Scant information exists on striped dolphins in the waters of Greece, except for a multitude of sighting and stranding reports (Frantzis et al. 2003; Frantzis 2009). The most detailed information comes from the semi-enclosed Gulf of Corinth—the subject of this thesis—where cetacean research conducted since the mid 1990s documented unusual mixed-species groups including striped and short-beaked common dolphins *Delphinus delphis*, as well as animals showing intermediate striped-common dolphin pigmentation (Frantzis and Herzing 2002; Frantzis et al. 2003; Bearzi et al. 2011a). Abundance of striped dolphins in the Gulf of Corinth was estimated as 835 animals in 2009 (95%CI 631–1,106; Bearzi et al. 2011a), but recent research has shown that actual numbers are much higher (mean 1,326 animals in years 2011–2015, 95%CI 1,179–1,490; Bearzi et al. in review). Striped and short-beaked common dolphins in the Gulf of Corinth are thought to be resident within the Gulf based on absence of records in the western sector as well as evidence from genetic studies (Bearzi et al. in review).

The objective of this thesis, based on data collected across five years of research effort from small boats, is to examine the distribution and habitat preferences of bottlenose and striped dolphins in the Gulf of Corinth, a semi-enclosed inland bay in central Greece. A modeling framework based on 13 explanatory variables was applied to investigate factors influencing dolphin distribution within the Gulf. Model output showed clear habitat preferences for both bottlenose and striped dolphins, thus ruling out the null hypothesis that the two species are randomly distributed.

This study 1) identifies relevant geographic, bathymetric, and environmental variables affecting the distribution of bottlenose and striped dolphins in the Gulf of Corinth; 2) compares these findings with information from other Mediterranean areas; 3) identifies anthropogenic factors likely to either affect dolphin distribution in the Gulf of Corinth (e.g. distance to fish farms), or imply direct or indirect exposure to potential threats (e.g. distance to patches of industrial byproducts dumped at sea); 4) frames these findings in the context of ongoing spatial management efforts in the region, advocating the inclusion of new information on dolphin habitat needs into future conservation action plans.

METHODS

Study area

The Gulf of Corinth is a deep semi-enclosed basin of approximately 2,400 km^2, separating the Peloponnese from mainland Greece (Figure 1). The Gulf is roughly 128 km long and up to 35 km wide. It is separated to the west from the outer Gulf of Patras and the Ionian Sea by the 1.9 km wide Rion-Antirion strait, and is bounded to the east by the Corinth Canal (25 m wide). The northern coast of the Gulf is dented by several large bays with few coastal towns, whereas the southern coast is mostly straight and more densely populated.

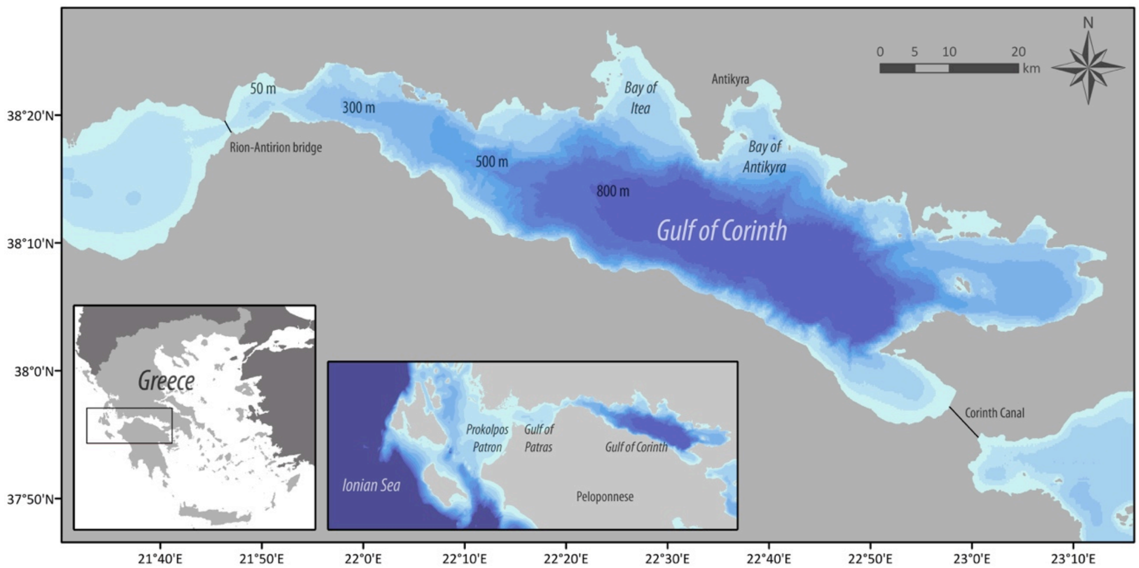

Figure 1. The Gulf of Corinth, showing depth contours and some of the locations cited in the text. Insets show the location of the Gulf in Greece (left) and the degree of separation between the deep inland waters of the Gulf and the deep open waters of the Ionian Sea (right).

The western sector of the Gulf leading to open Ionian Sea (and Mediterranean) waters is relatively shallow (Figure 1), with a maximum depth of 65 m under the Rion-Antirion bridge.

The central sector includes a large basin with depths of 500–900 m. The waters of the Gulf are mostly oligotrophic and transparent, with Secchi disk readings of 10–33 m (Bearzi et al. 2011a).

The Gulf is exposed to discharges of ephemeral streams (there are no major rivers), runoff from extensive agriculture (Botsou and Hatzianestis 2012), sewage from coastal cities and industrial discards. The main concern is related to an aluminum processing plant—Aluminum of Greece S.A.—which has been operating since 1966 on the northern coast (www.alhellas.com; Figure 7). The tailing—a by-product of bauxite processing known as 'red mud' (largely composed of oxides of Fe, Al and Ti)—was discarded by barges in waters <50 m deep until 1969. Increase in industrial production led to the construction of underwater pipelines discarding red mud at depths between 120 and 265 m (Iatrou 2013). Between 500,000 and 700,000 tonnes of red mud have been disposed annually into the Gulf (Varnavas et al. 1986; Varnavas and Achilleopoulos 1995; Papatheodorou et al. 1999; Pontikes 2007), resulting in two main deposits on the sea floor (Iatrou 2013, p. 171). These include a coastal deposit situated in the Bay of Antikyra, covering 36.5 km^2 (with an estimated total volume of 40 million m^3), and an offshore deposit in the central part of the Gulf, covering 288 km^2 (with an estimated total volume of about 2 million m^3; Figure 7). Dumping at sea was reported to have stopped in 2011, red mud being currently disposed on land (Issaris et al. 2012; www.alhellas.com visited 31 December 2015).

Research context

Research for this thesis was conducted in the context of a longitudinal study of dolphin ecology, which was initiated in 2009 and is ongoing. The study has been relying extensively on individual photo-identification and photographic capture-recapture methods, which yielded information on dolphin abundance and status (Bearzi et al. 2011a, 2016, in review; Santostasi et al. 2015, 2016). As the principal field investigator in years 2011–2015, I was in charge of data collection at sea and participated in all the boat surveys. Additionally, I was in charge of database management. These factors ensured homogeneous gathering and treatment of information, which helped minimize observer-dependent and other biases.

Survey effort

Boat-based visual surveys were conducted from a 5.8 m inflatable boat with rigid hull powered by a 100 HP four-stroke outboard engine, between May and October 2011–2015, totaling 211 days at sea and 21,435 km of navigation (Table 1, Figure 2). Navigation was carried out under the following conditions: 1) daylight and no fog; 2) sea state ≤2 Douglas; 3) at least two experienced observers scanning the sea surface by naked eye; 4) eye elevation of 1.6–1.8 m for both observers; and 5) survey speeds between 26 and 31 km h^{-1}. A survey was interrupted if dolphins were sighted, sea or weather conditions deteriorated, or other factors (e.g. late hour) forced the crew to return to port. Binoculars were not used during navigation. Survey routes varied depending primarily on sea conditions, but attempts were made to obtain a homogeneous coverage of the study area. Navigation under "favorable conditions" (sea states S1, S2 and S3 as described in the 'Effort index and sea state' section) totaled 14,148 km, i.e. 66% of total navigation effort. The boat's position was recorded via GPS at 1 min intervals throughout navigation and dolphin group follows, for a total of 68,913 data points.

During a dolphin sighting, the vessel moved parallel to and at the same speed as the dolphin group, in an attempt to minimize disturbance. Dolphin movements were tracked using the vessel's GPS position as a proxy for dolphin position. Navigation and dolphin follow data were retrieved from the GPS using MapSource 6.16.3. Additional information, including time, geographic position, track length, and speed, was automatically recorded by the GPS, downloaded via MapSource (Figure 3), and then saved in Excel format.

Year	2011	2012	2013	2014	2015	Total
# months	3	5	5	5	6	24
# days at sea	31	28	49	52	51	211
km of total survey effort	4,171	3,362	4,243	4,514	5,145	21,435
km of favorable survey effort	3,056	2,380	2,552	3,050	3,110	14,148
km with bottlenose dolphins	17	53	84	104	77	335
km with striped dolphins	316	342	450	382	383	1,873
hours spent at sea	214	210	287	304	329	1,344
hours spent with bottlenose dolphins	3	9	16	22	16	66
hours spent with striped dolphins	51	53	76	65	65	311

Table 1. Summary of research effort and data collected in 2011–2015.

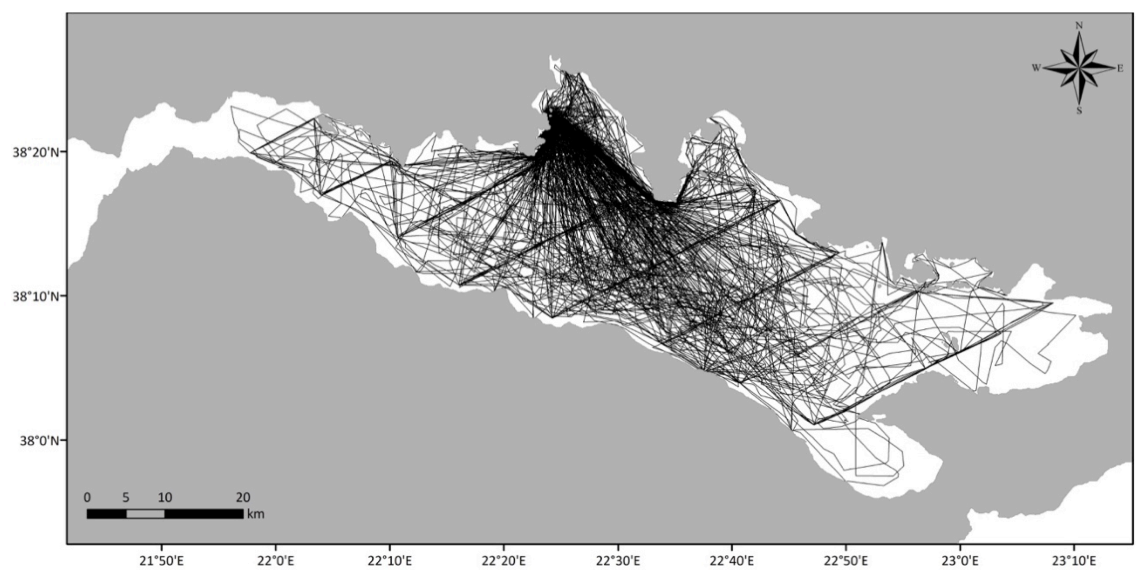

Figure 2. Gulf of Corinth: total survey effort conducted in 2011-2015 (black track lines).

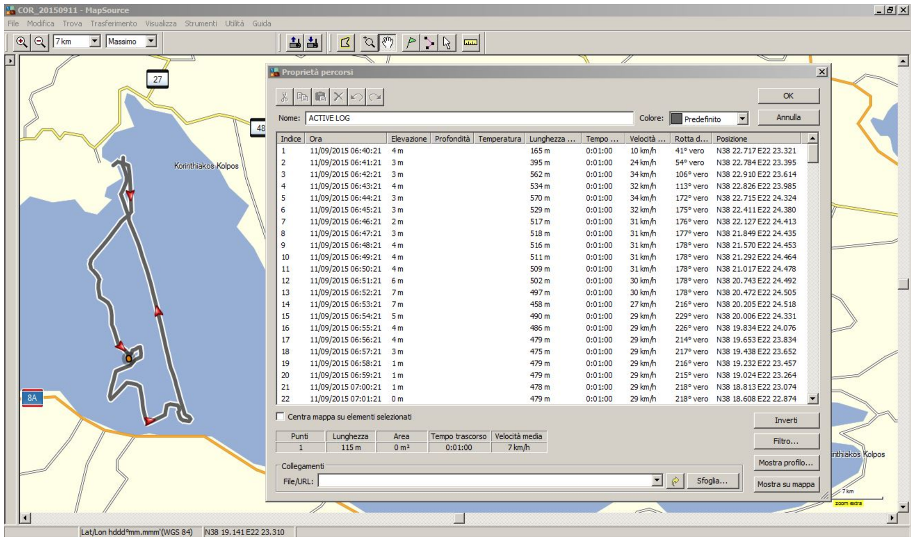

Figure 3. MapSource layout showing an example of survey route with additional information associated with each 1-min GPS position.

An Excel database was used to store information related to the single 1-min GPS positions, following Bonizzoni et al. (2014), which was combined with additional log data recorded on a digital tape recorder throughout the surveys. Once all navigation and dolphin follow data were merged with the log notes recorded on tape, and carefully verified to check for mistakes, all data were transferred to ArcMap 10.3.

Effort index and sea state

To account for a different probability of encountering dolphins depending on different effort and sea state conditions (Buckland et al. 2001; Evans and Hammond 2004), two variables were created and included in all models: "effort index" and "sea state", following Bonizzoni et al. (2014).

The entire study area was divided into grid cells of 4 x 4 km, a scale consistent with the resolution of satellite data, yielding a total of 173 data cells (Figure 4). Within each cell, a sampling effort index was generated by calculating the number of sampling points divided by the water surface area available to dolphins, taking into account the coastal profile (Bonizzoni et al. 2014). The sampling effort index was then simplified into a factor variable at the quartiles of the resulting values, generating categories of 'low', 'medium', 'high', and 'very high' survey effort. GPS points with boat floating adrift or crew not actively searching for dolphins were removed from the analysis.

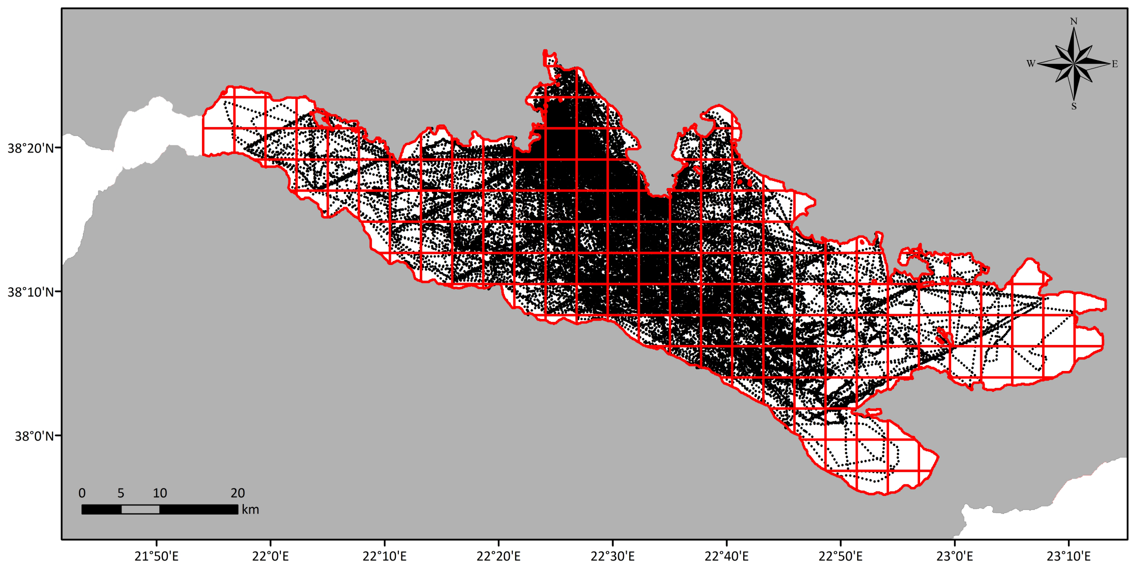

Figure 4. Data points used for this study (black), with super-imposed grid cells of 4 x 4 km (red) used to account for different survey effort within each cell.

As sea conditions are known to affect dolphin detectability (Buckland et al. 2001; Evans and Hammond 2004), sea state was categorized as follows: S1 (flat), S2 (calm but rippled), S3 (non-breaking wavelets less than 20 cm high). Data collected with sea states above S3 (breaking waves), accounting for 10% of total favorable navigation, were removed from the analysis due to the low probability of spotting dolphins under those conditions. Data collected during dolphin group follows under sea states above S3, accounting for 4.1% (bottlenose dolphin dataset) and 3.8% (striped dolphin dataset) of total data points, were similarly removed from the analysis.

Units of analysis and data sources

Group follows data and survey data were both included in distribution models, following Pirotta et al. (2011) and Bonizzoni et al. (2014). Each 1-min position was then related to the variables shown in Table 2.

Variable	Source
Presence/absence of dolphins	Field data
Sea state	Field data
Effort index	Field data
Latitude	Field data
Longitude	Field data
SST	Online database
Chl-*a*	Online database
Bottom depth	Online database
Bottom slope	ArcMap
Distance to nearest coast	ArcMap
Distance to nearest upwelling area	ArcMap
Distance to nearest fish farm	ArcMap
Distance to coastal red mud deposit	ArcMap
Distance to offshore red mud deposit	ArcMap

Table 2. Variables considered in the modeling.

All GPS points were divided into individual blocks defined as the set of continuous search points up to a dolphin sighting, or the set of points associated with a dolphin group follow, following Pirotta et al. (2011). A new block was also started with each day of sampling. These blocks were then analyzed to account for the autocorrelation between residuals within blocks.

The dataset was split into two subsets, one including data points with navigation and bottlenose dolphin group follows and one including data points with navigation and striped dolphin group follows. Consequently, all GPS points related to the presence of striped dolphins were removed from the bottlenose dolphin subset, and vice versa. In each data subset, GPS points characterized by unfavorable conditions (observers not looking for dolphins, or sea state above S3, or non-standard navigation conditions) were removed from the analyses (Pirotta et al. 2011; Bonizzoni et al. 2014). Table 3 summarizes which GPS points were considered or removed from the modeling process. A total of 40,457 data points were considered in the bottlenose dolphin dataset, and 55,513 points in the striped dolphin dataset.

Species dataset	Condition	Species presence / absence	GPS data point decision
Bottlenose dolphin	Unfavorable	Bottlenose dolphin absence	remove
	Unfavorable	Striped dolphin presence	remove
	Favorable	Bottlenose dolphin absence	consider
	Favorable	Bottlenose dolphin presence	consider
Striped dolphin	Unfavorable	Striped dolphin absence	remove
	Unfavorable	Bottlenose dolphin presence	remove
	Favorable	Striped dolphin absence	consider
	Favorable	Striped dolphin presence	consider

Table 3. Decision-making process leading to inclusion or exclusion of GPS data points in the modeling process.

Satellite data for SST and Chl-*a* were obtained from NASA OceanColor Web Level 3 Browser (oceancolor.gsfc.nasa.gov) as monthly averages MODIS-SMI (Moderate Resolution Imaging Spectroradiometer - Standard Mapped Image) products at 4 km spatial resolution. Upwelling spots were identified as areas with simultaneously below-average SST and above-average Chl-*a* values (Valavanis et al. 2004). Bottom depth was obtained from the European Marine Observation and Data Network (EMODNET, www.emodnet-hydrography.eu) as gridded data interpolated to 0.002 decimal degrees (approximately 220 m). All datasets were converted to ArcGIS grid format and then interpolated using ArcGIS topogrid tool at a common spatial resolution of 220 m—a scale consistent with the resolution of the sampled data.

All GPS points for navigation and group follows were associated with 13 explanatory variables: 1) effort index; 2) sea state; 3) latitude; 4) longitude; 5) bottom depth; 6) bottom slope; 7) distance to nearest coast; 8) sea surface temperature (SST); 9) chlorophyll-*a* (Chl-*a*); 10) distance to nearest upwelling area; 11) distance to nearest fish farm; 12) distance to coastal red mud deposit; 13) distance to offshore red mud deposit.

Each survey data point and dolphin follow position data point was related to the quantitative variables considered in the modeling, by using the "extract multi values to points" tool available in ArcGIS software (ESRI ArcMap 10). Examples of layout layers used in ArcMap to extrapolate data to be associated to each 1-min GPS positions are shown in Figure 5.

Bottom depth and distances were measured in meters, bottom slope in degrees, SST in degrees Celsius, and Chl-*a* in mg/m^3. Bottom slope and distances were calculated via spatial analyst tools using GIS software (ESRI ArcMap 10).

Visual inspections by boat, information gathered from Google Earth and nautical charts were used to locate all aquaculture facilities in the Gulf. This procedure yielded 17 fish farms that were inspected visually and confirmed to be active (Figure 6). The geometry of each fish farm was mapped by GPS while circumnavigating the farm with our boat. Farmed fish species included European sea bass *Dicentrarchus labrax* and gilthead sea bream *Sparus aurata* (Thomas Siarmpas, Galaxidi Marine Farm S.A., personal communication).

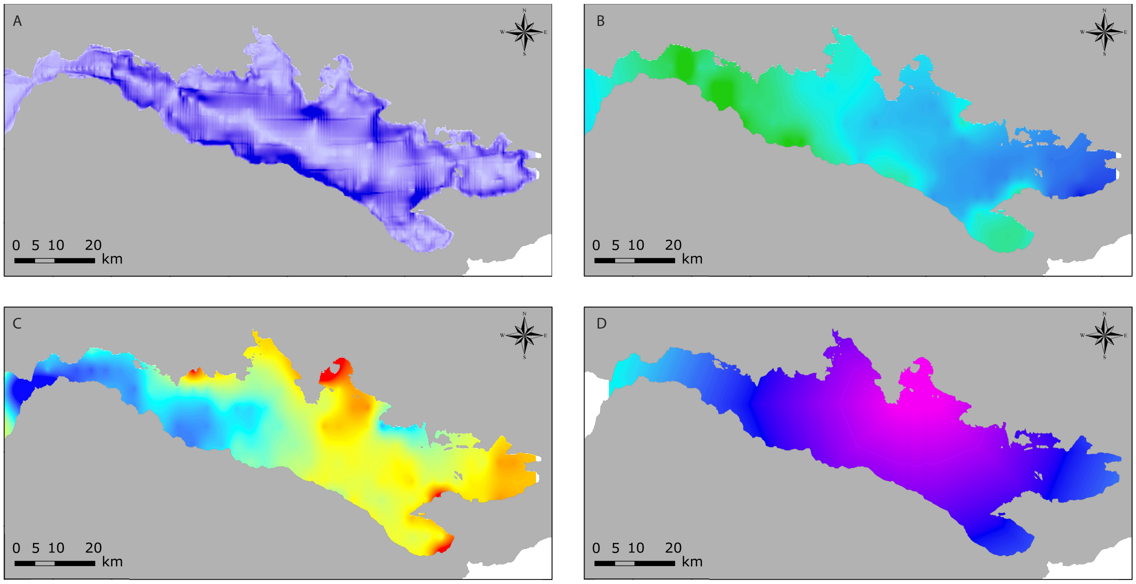

Figure 5. Visualization of some of the layers used in ArcMap to obtain data for modeling analyses: (A) bottom slope (light violet indicates flat bottom, dark violet indicates steep bottom areas), (B) Chl-*a* monthly average (green indicates high Chl-*a* concentration, dark blue indicates low concentration), (C) SST monthly average (red indicates warm areas, dark blue cold areas), (D) distance to coastal red mud deposit (pink identifies proximity to the deposit, light blue areas away from the deposit).

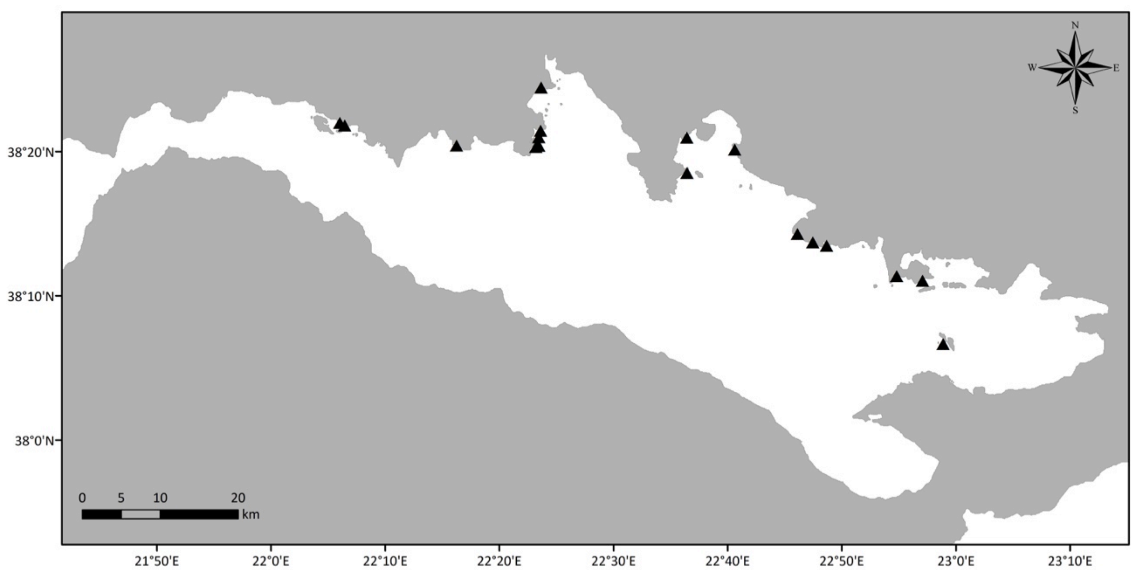

Figure 6. Location of 17 active fish farms in the Gulf of Corinth (black triangles).

Distance to red mud deposits was based on georeferencing of a map provided by Iatrou (2013, p. 171), which was obtained from marine geophysical exploration comprising sub-bottom profiler, echo-sounder, side scan sonar systems and visual inspection of the seafloor using a remotely-operated vehicle. The location of the coastal and offshore red mud deposits is shown in Figure 7.

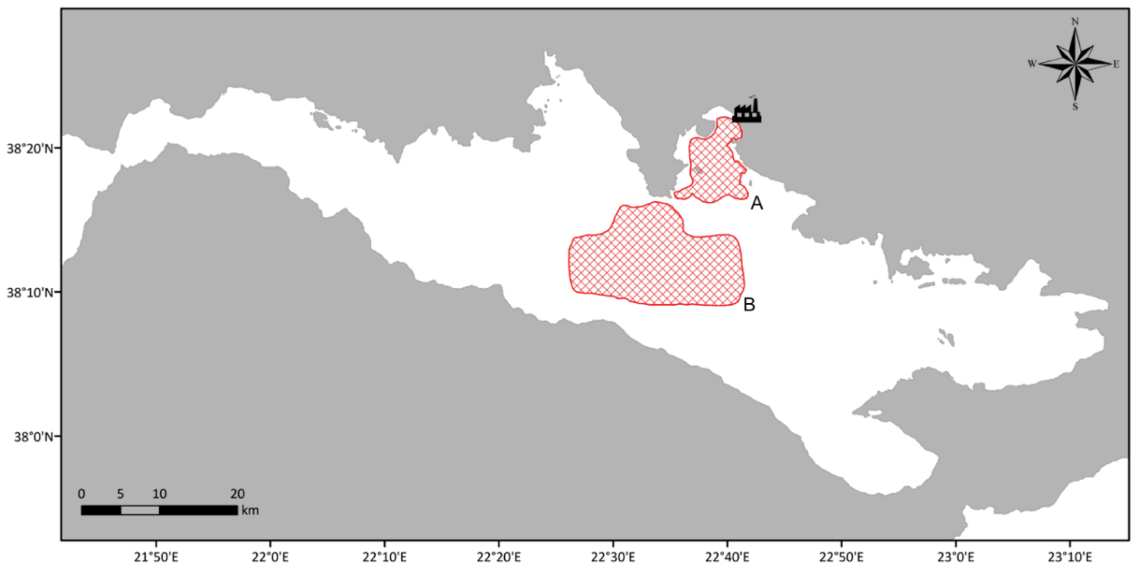

Figure 7. Location of coastal (A) and offshore (B) red mud deposits, based on Iatrou (2013). The position of the aluminum factory is indicated by a factory icon.

All distances to anthropogenic features—fish farms and red mud deposits—were calculated as minimum distances to the perimeter of the feature, also taking into account the coastal profile, by using the "cost-distance function" within ArcGIS (ESRI ArcMap 10).

Modeling framework

To investigate the factors affecting the distribution of dolphins in the Gulf of Corinth, a generalized additive modeling (GAM) framework was employed (Table 4). GAMs are a non-parametric extension of general linear models (GLMs), and allow for flexible relationships between the response variable and explanatory variables (Hastie and Tibshirani 1990; Wood 2006). Here, binomial GAMs with a logit link were employed. The logit link function converts the probability of dolphin presence to the natural logarithm of the odds, and thus enables this probability to be modeled as a function of the covariates on a linear scale (Matthiopoulos 2011). To allow the use of all collected data, generalized estimation equations (GEEs) were used in combination with GAMs, in an approach similar to Pirotta et al. (2011) and Bonizzoni et al. (2014). Three model correlation structures were investigated based on different correlation structure estimator (AR1, exchangeable, independence); a simple working independence model structure performed better than the others (as also advised by Pan 2001) and it was chosen to be used in the modeling process.

Pairwise scatterplots were used to assess correlation between the explanatory variables in the bottlenose dataset (Figure 8) and the striped dolphin dataset (Figure 9). Nominal variables (dolphin presence, effort index and sea state) were not included in the plots, as suggested by Zuur et al. (2009).

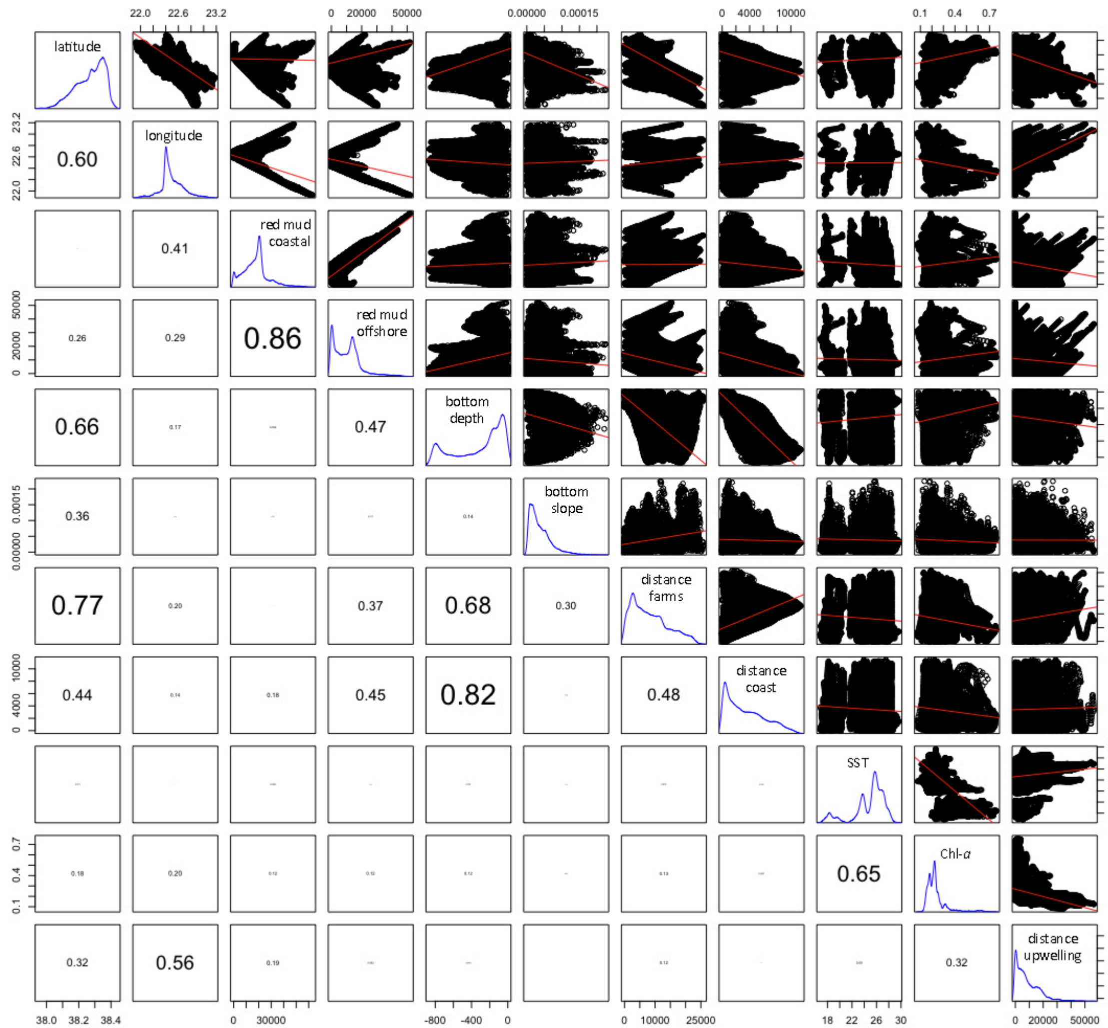

Figure 8. Pairplot of all the quantitative explanatory variables considered in the bottlenose dolphin dataset. The lower panel (with numbers) contains pairwise correlations and the font size is proportional to the absolute value of the estimated correlation coefficient. The upper panel contains scatterplots.

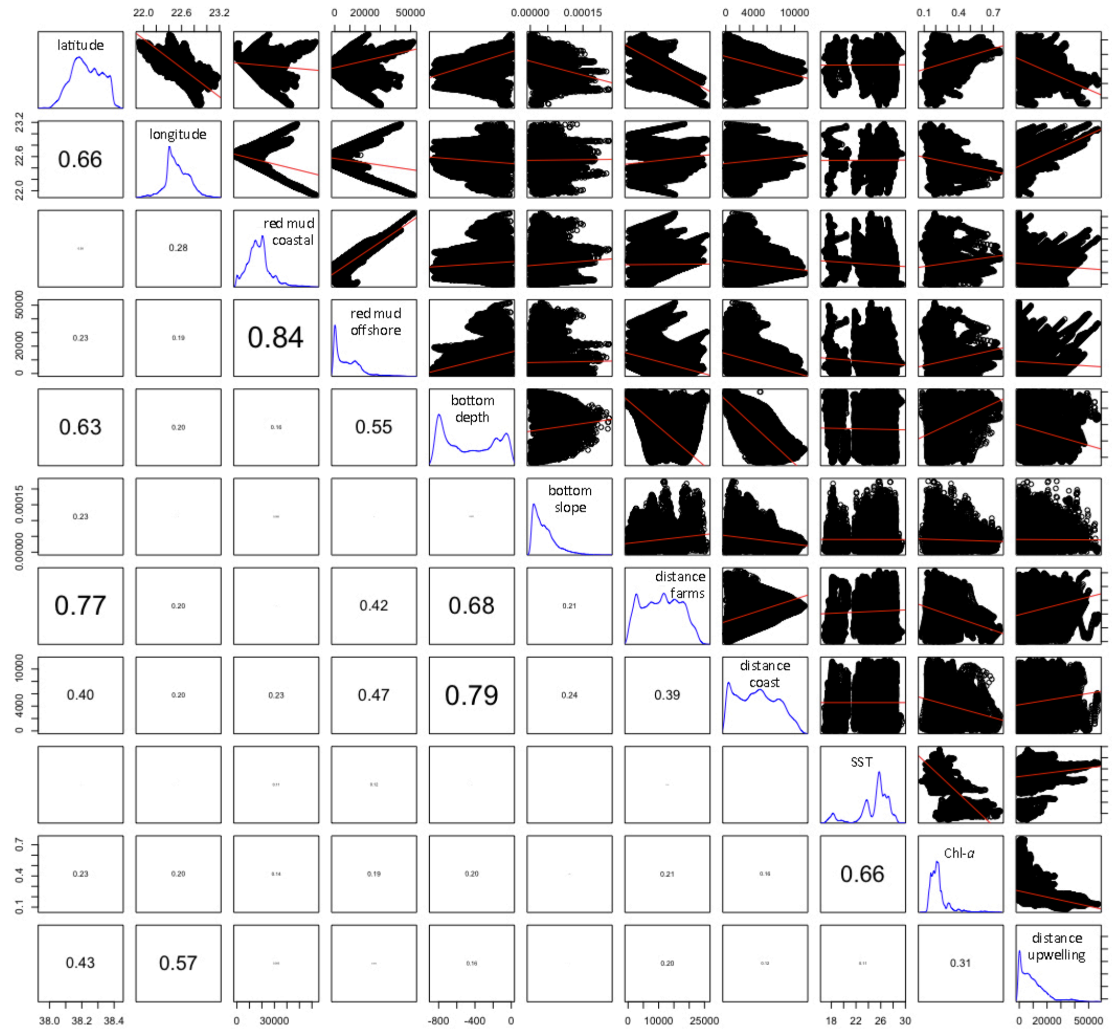

Figure 9. Pairplot of all the quantitative explanatory variables considered in the striped dolphin dataset. The lower panel (with numbers) contains pairwise correlations and the font size is proportional to the absolute value of the estimated correlation coefficient. The upper panel contains scatterplots.

To address overfitting issues highlighted by an initial model exploration, and to determine types of factors influencing dolphin occurrence, four different submodels with a specific set of explanatory variables were used. Using several models rather than a single one allowed to 1) compare models of relatively equal fit; 2) have complementary models rather than competing ones (Planque et al. 2011); and 3) prevent incorrect interpretation of particular effects and their influence on animal distribution (Loots et al. 2011). The sub-model framework used in this study is shown in Table 4. All submodels include effort index and sea state to account for sampling bias.

Geographic model	Bathymetric model	Environmental model	Anthropogenic model
Effort index	Effort index	Effort index	Effort index
Sea state	Sea state	Sea state	Sea state
Latitude	Bottom depth	SST	Distance to nearest fish farm
Longitude	Bottom slope	Chl-*a*	Distance to coastal red mud deposit
	Distance to nearest coast	Distance to nearest upwelling area	Distance to offshore red mud deposit

Table 4. Framework of explanatory variables considered in four submodels.

Before model selection, multicollinearity was investigated in all four submodels by using the variance inflation factor (VIF). Explanatory variables with VIF >4 were removed from the submodel, so that the remaining variables were not correlated (Neter et al. 1990; Booth et al. 1994). Generalized linear models (GEE-GLMs) were constructed with R package (R Development Core Team 2014), using geepack (Højsgaard et al. 2006). The package splines (R

Development Core Team 2014) were then used to build smoothing splines within the GEE-GLMs, generating GEE-GAMs. Models were fitted using package mgcv version 1.8-4 for R (Wood 2014). To prevent overfitting, each explanatory variable was given a maximum number of degrees of freedom (df) to restrict flexibility as suggested by Ciannelli et al. (2008). Explanatory variables in the geographic, bathymetric and environmental models were constrained to 3 df per continuous fit, while anthropogenic variables were given 4 df to provide more flexibility. The importance of variables was investigated by using a manual backward stepwise selection procedure. The resulting models were compared by the percent deviance explained and the quasi-likelihood under the independence model criterion (QIC).

RESULTS

Dolphin occurrence and movements

Dolphins were observed on 158 of 211 days spent at sea, and followed between 6 AM and 10 PM across a total of 2,208 km and 377 h.

Bottlenose dolphins were observed on 45 days, for a total of 53 sightings. Bottlenose dolphin group follows lasted for a mean of 76 min (SD = 77.3, range 1–396), totaling 67 h 10 min. Recorded movements totaled 336 km. Bottlenose dolphins were encountered and tracked only in the northern-central part of the Gulf, except for one sighting that occurred along the south-western coast (Figure 10). Of 40,457 GPS points considered (see Table 3 in "Units of analysis and data sources") 4,087 were associated with bottlenose dolphin presence. This species was often found in proximity to fish farms (Figure 6), with a mean distance from the closest farm of 3.4 km (SD = 2.88, n = 4,087). Bottlenose dolphins were mainly encountered and followed in shallow continental shelf waters, with a maximum distance to the nearest coast of 6.0 km (mean = 1.4 km, SD = 1.30, n = 4,087). Maximum bottom depth was 353 m (mean = 90 m, SD = 58.9, n = 4,087).

Striped dolphins were observed on 132 days, for a total of 475 sightings. Striped dolphin group follows lasted for a mean of 40 min (SD = 44.6, range 1–309), totaling 309 h and 57 min. Recorded movements totaled 1,759 km. Of 55,513 GPS points considered (see Table 3 in "Units of analysis and data sources"), 19,143 were associated with striped dolphin presence. Striped dolphins were mainly encountered in the central portion of the Gulf (Figure 10). However, they occasionally approached the coast (minimum distance 0.28 km). Striped dolphin mean distance from the coast was 6.1 km (SD = 2.37, n = 19,143), and mean bottom depth was 660 m (SD = 176.4, max = 868, n = 19,143).

Tables 5 and 6 provide an overview of the quantitative explanatory variables when bottlenose and striped dolphins were present.

Explanatory variable	mean	SD	range
SST (°C)	25.3	2.03	18.3–29.6
Chl-*a*	0.24	0.09	0.14–0.63
Bottom depth (m)	-90	58.97	-353–0
Bottom slope (degrees)	$2.4x10^{-5}$	$1.7x10^{-5}$	$0–1.1x10^{-4}$
Distance to nearest coast	1,428	1,302.30	0–6,053
Distance to nearest fish farm	3,423	2,876.23	0–13,383
Distance to upwelling areas	10,270	8,190.73	0–31,373
Distance to coastal red mud deposit	16,456	8,542.22	0–38,127
Distance to offshore red mud deposit	12,113	5,245.32	0–24,338

Table 5. Overview of quantitative explanatory variables: bottlenose dolphins.

Explanatory variable	mean	SD	range
SST (°C)	25.1	2.47	17.2–28.5
Chl-*a*	0.21	0.07	0.12–0.59
Bottom depth (m)	-660	176.44	-868–0
Bottom slope (degrees)	$0.4x10^{-4}$	$3.3x10^{-5}$	$0–2.2x10^{-4}$
Distance to nearest coast	6,145	2,371.85	281–11,463
Distance to nearest fish farm	14,752	4,207.21	1,945–23,961
Distance to upwelling areas	11,728	10,429.49	0–56,764
Distance to coastal red mud deposit	16,969	6,717.37	1,4250–40,988
Distance to offshore red mud deposit	5,001	6,450.10	0–36,588

Table 6. Overview of quantitative explanatory variables: striped dolphins.

Bottlenose and striped dolphin movements suggest habitat partitioning, and the two species were never observed in mixed-species groups, or at the same time in the same area (Figure 10).

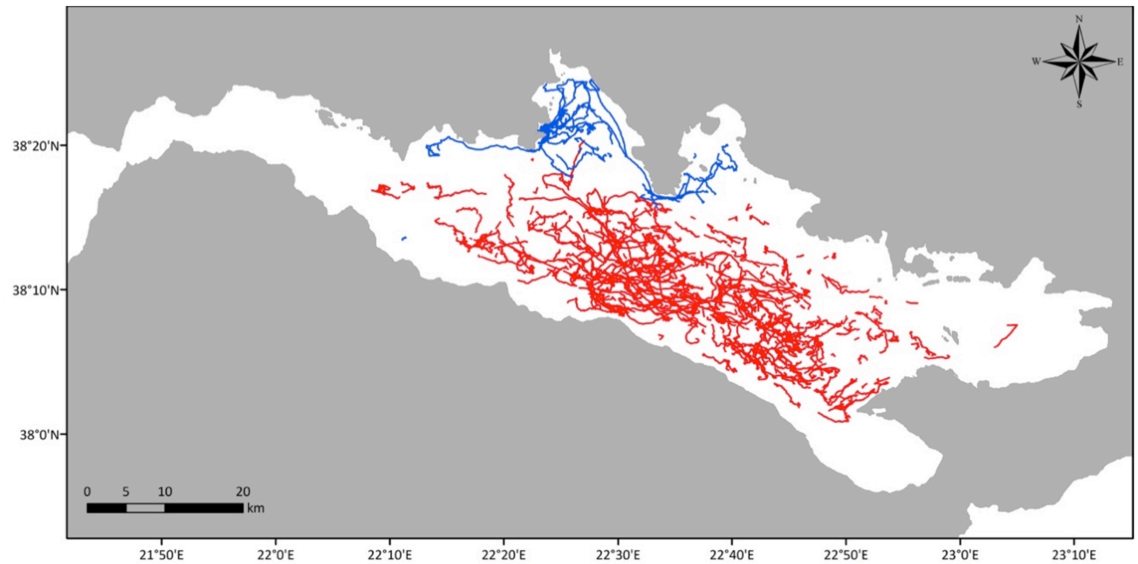

Figure 10. Movements of bottlenose dolphins (blue) and striped dolphins (red) tracked in the Gulf of Corinth between 2011 and 2015.

<u>*Model output: bottlenose dolphins*</u>

Table 7 shows QIC model values used to identify explanatory variables to be considered in the final submodels for bottlenose dolphins.

The geographic submodel retained both latitude and longitude (Figure 11). Bottlenose dolphin occurrence was higher in the northern portion of the Gulf, though values below 38.2°N should be interpreted with caution considering wide confidence intervals. Although longitude was retained, its response curve shows wide confidence intervals throughout, and no influence is apparent.

Within the bathymetric submodel, bottom depth and bottom slope were retained, while distance to nearest coast was removed via the QIC model selection procedure. The response curve for depth suggests higher bottlenose dolphin occurrence in waters shallower than approximately 300 m, while the response curve for slope indicates a possible avoidance of steep bottom contours (Figure 12).

In the environmental submodel, both SST and Chl-*a* were dropped, while distance to the closest upwelling area was retained. Its response curve suggests a lower bottlenose dolphin occurrence at distances greater than 40 km from upwelling areas, but confidence intervals past this value are wide (Figure 13).

In the anthropogenic model, distance to the offshore red mud deposit was removed due to collinearity issues. Distance to the coastal red mud deposit and sea state were not retained. The final sub-model strongly indicates that bottlenose dolphin occurrence is higher in areas within approximately 10 km of fish farms, with a peak in their immediate proximity (Figure 13).

Submodel	Bottlenose dolphin occurence explained by	QIC value	
geographic	latitude+longitude+sea.state+effort.index	20655	
	latitude+sea.state+effort.index	20838	
	longitude+sea.state+effort.index	23392	
	latitude+longitude+effort.index	20611	
	latitude+longitude+effort.index	20552	
	longitude+sea.state	24164	
	latitude+sea.state	21093	
	latitude+longitude	20514	*
	longitude	24126	
	latitude	20962	
bathymetric	bathymetry+slope+distance.coast+sea.state+effort.index	20365	
	slope+distance.coast+sea.state+effort.index	20982	
	bathymetry+distance.coast+sea.state+effort.index	20570	
	bathymetry+slope+sea.state+effort.index	20139	
	bathymetry+slope+distance.coast+sea.state	20351	
	bathymetry+slope+distance.coast+effort.index	20176	
	slope+sea.state+effort.index	22984	
	bathymetry+sea.state+effort.index	20287	
	bathymetry+slope+effort.index	19965	*
	bathymetry+slope+sea.state	20144	
	slope+effort.index	22898	
	bathymetry+effort.index	20124	
	bathymetry+slope	19979	
environmental	SST+Chla+distance.upwelling+sea.state+effort.index	23994	
	Chla+distance.upwelling+sea.state+effort.index	23751	
	SST+distance.upwelling+sea.state+effort.index	23841	
	SST+Chla+sea.state+effort.index	24340	
	SST+Chla+distance.upwelling+effort.index	23913	
	SST+Chla+distance.upwelling+sea.state	25651	
	distance.upwelling+sea.state+effort.index	23418	*
	Chla+sea.state+effort.index	24013	
	Chla+distance.upwelling+effort.index	23682	
	Chla+distance.upwelling+sea.state	25786	
anthropogenic	distance.farm+distance.redmud.coastal+sea.state+effort.index	20964	
	distance.redmud.coastal+sea.state+effort.index	22726	
	distance.farm+sea.state+effort.index	20672	
	distance.farm+distance.redmud.coastal+effort.index	20912	
	distance.farm+distance.redmud.coastal+sea.state	20932	
	sea.state+effort.index	23560	
	distance.farm+effort.index	20640	*
	distance.farm+sea.state	20968	
	effort.index	23490	
	distance.farm	20920	

Table 7. QIC values of the submodels considered for the bottlenose dolphin dataset. In each category (geographic, bathymetric, environmental and anthropogenic), the best submodel (indicated with *) was obtained through backward selection process and identified by the lowest QIC value.

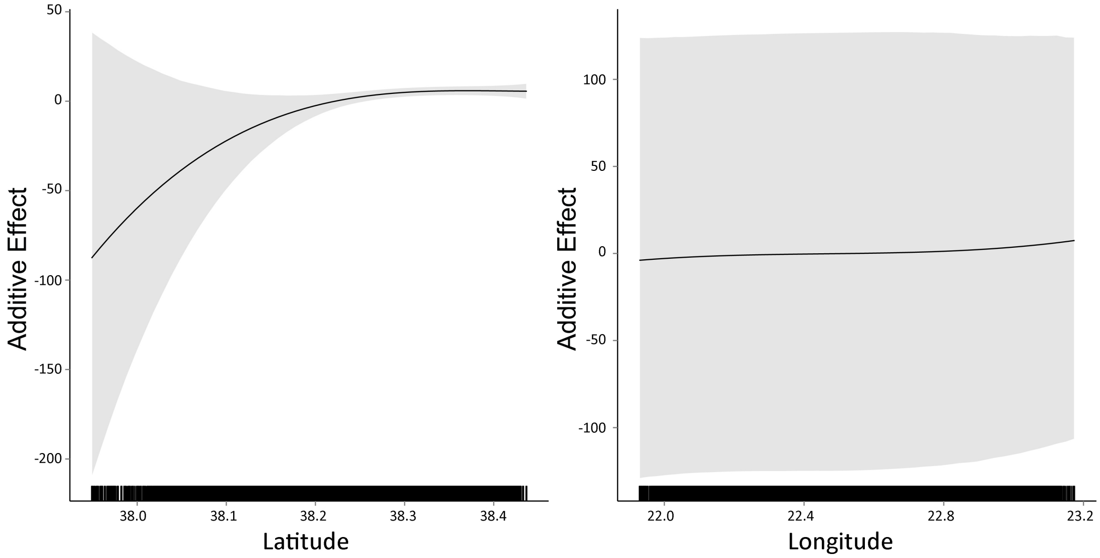

Figure 11. Response curves of the relationship between bottlenose dolphin occurrence and latitude (left), and between bottlenose dolphin occurrence and longitude (right). Zero on the vertical axis corresponds to no effect of the covariate on the estimated response. Positive values on the vertical axis correspond to a positive relationship between the covariate and occurrence of dolphins, while negative values correspond to a negative relationship. Shaded areas represent 95%CI as calculated by GEE.

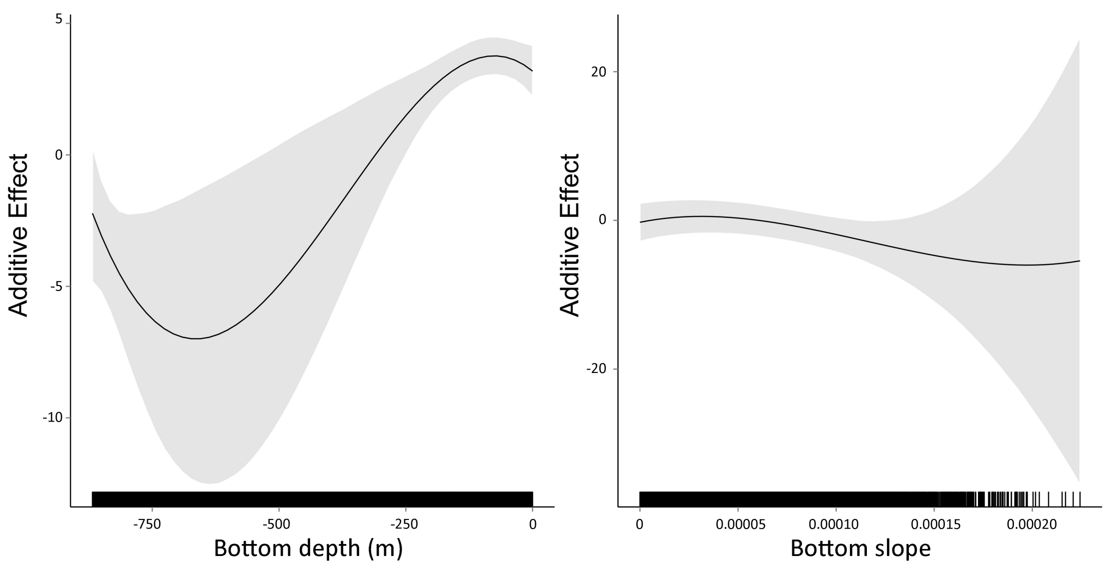

Figure 12. Response curves of the relationship between bottlenose dolphin occurrence and bottom depth (left), and between bottlenose dolphin occurrence and bottom slope (right). Zero on the vertical axis corresponds to no effect of the covariate on the estimated response. Positive values on the vertical axis correspond to a positive relationship between the covariate and occurrence of dolphins, while negative values correspond to a negative relationship. Shaded areas represent 95%CI as calculated by GEE.

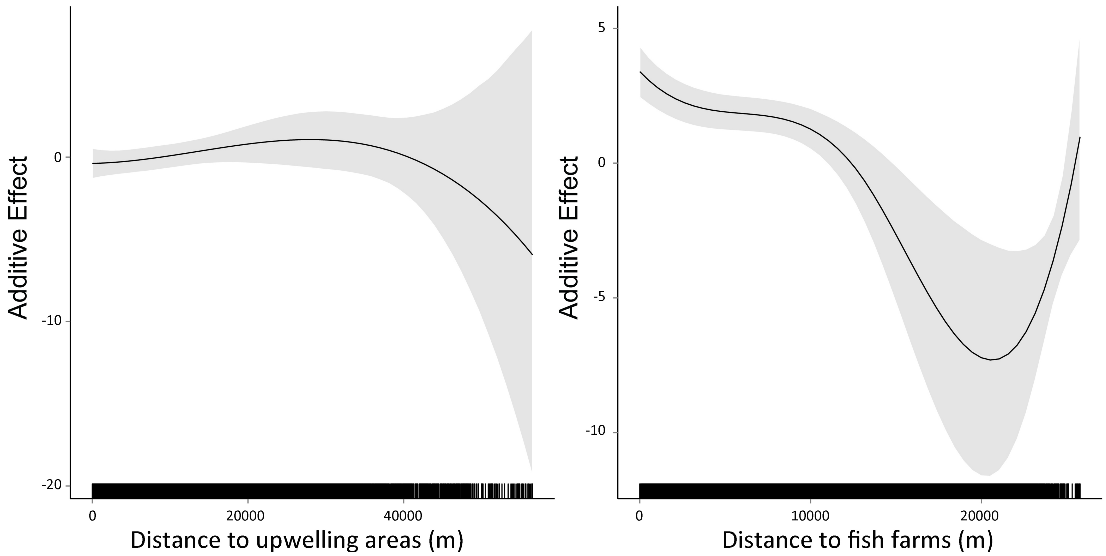

Figure 13. Response curves of the relationship between bottlenose dolphin occurrence and distance to upwelling areas (left), and bottlenose dolphin occurrence and distance to fish farms (right). Zero on the vertical axis corresponds to no effect of the covariate on the estimated response. Positive values on the vertical axis correspond to a positive relationship between the covariate and occurrence of dolphins, while negative values correspond to a negative relationship. Shaded areas represent 95%CI as calculated by GEE.

Model output: striped dolphins

The geographic submodel for striped dolphins retained both latitude and longitude. Occurrence of striped dolphins appears to be higher in the central and southern sectors of the Gulf of Corinth, whereas it drops in its northern portion (Figure 14). Longitude has wide confidence intervals, especially towards to west part of the Gulf (Figure 14), and model output is poorly informative in this case, also considering that no observations ever occurred west of 22.14°E.

Only bottom depth was retained within the bathymetric submodel. Striped dolphins clearly prefer waters deeper than 300 m, with a steady increase of occurrence as bottom depth increases (Figure 15).

In the environmental submodel, both SST and distance to upwelling areas were dropped, while Chl-*a* was retained. The response curve suggests that striped dolphin occurrence is negatively affected by Chl-*a* concentration (Figure 15), suggesting a preference for oligotrophic waters.

The anthropogenic submodel retained distance to fish farms, with increased occurrence of striped dolphins in the range of approximately 10–22 km from the facilities. Distance to the coastal red mud deposit was removed due to collinearity issues, whereas distance to the offshore red mud deposit was retained. The response curve suggests that striped dolphins do not avoid the offshore red mud area (Figure 16).

Submodel	Striped dolphin occurence explained by	QIC value	
geographic	latitude+longitude+sea.state+effort.index	48622	
	latitude+sea.state+effort.index	49369	
	longitude+sea.state+effort.index	54830	
	latitude+longitude+effort.index	48842	
	latitude+longitude+sea.state	48570	*
	longitude+sea.state	61523	
	latitude+sea.state	49322	
	latitude+longitude	48794	
bathymetric	bathymetry+slope+distance.coast+sea.state+effort.index	49040	
	slope+distance.coast+sea.state+effort.index	51709	
	bathymetry+distance.coast+sea.state+effort.index	49010	
	bathymetry+slope+sea.state+effort.index	48852	
	bathymetry+slope+distance.coast+sea.state	49905	
	bathymetry+slope+distance.coast+effort.index	49183	
	slope+sea.state+effort.index	57440	
	bathymetry+sea.state+effort.index	48820	*
	bathymetry+slope+effort.index	48995	
	bathymetry+slope+sea.state	49704	
	sea.state+effort.index	57751	
	bathymetry+effort.index	48968	
	bathymetry+sea.state	49645	
environmental	SST+Chla+distance.upwelling+sea.state+effort.index	57603	
	Chla+distance.upwelling+sea.state+effort.index	57405	
	SST+distance.upwelling+sea.state+effort.index	57495	
	SST+Chla+sea.state+effort.index	57551	
	SST+Chla+distance.upwelling+effort.index	57996	
	SST+Chla+distance.upwelling+sea.state	64694	
	distance.upwelling+sea.state+effort.index	57462	
	Chla+sea.state+effort.index	57225	*
	Chla+distance.upwelling+effort.index	57759	
	Chla+distance.upwelling+sea.state	64684	
	sea.state+effort.index	57751	
	Chla+effort.index	57554	
	Chla+sea.state	64615	
anthropogenic	distance.farm+distance.redmud.offshore+sea.state+effort.index	49082	*
	distance.redmud.offshore+sea.state+effort.index	53408	
	distance.farm+distance.redmud.offshore+sea.state+effort.index	50311	
	distance.farm+distance.redmud.offshore+effort.index	49301	
	distance.farm+distance.redmud.offshore+sea.state	51449	

Table 8. QIC values of the submodels considered for the striped dolphin dataset. In each category (geographic, bathymetric, environmental and anthropogenic), the best submodel (indicated with *) was obtained through backward selection process and identified by the lowest QIC value.

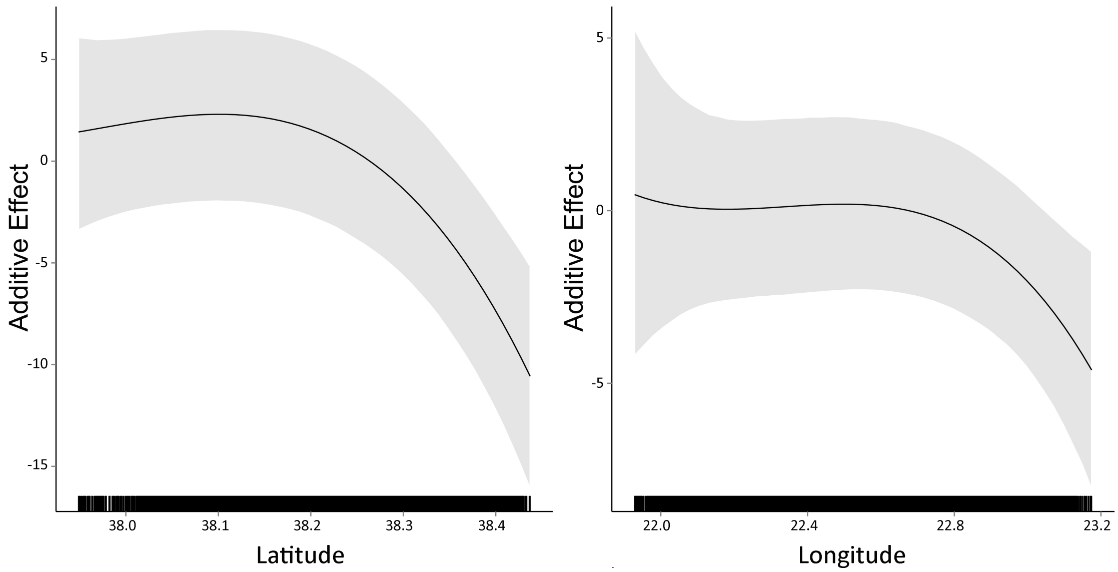

Figure 14. Response curves of the relationship between striped dolphin occurrence and latitude (left), and between striped dolphin occurrence and longitude (right). Zero on the vertical axis corresponds to no effect of the covariate on the estimated response. Positive values on the vertical axis correspond to a positive relationship between the covariate and occurrence of dolphins, while negative values correspond to a negative relationship. Shaded areas represent 95%CI as calculated by GEE.

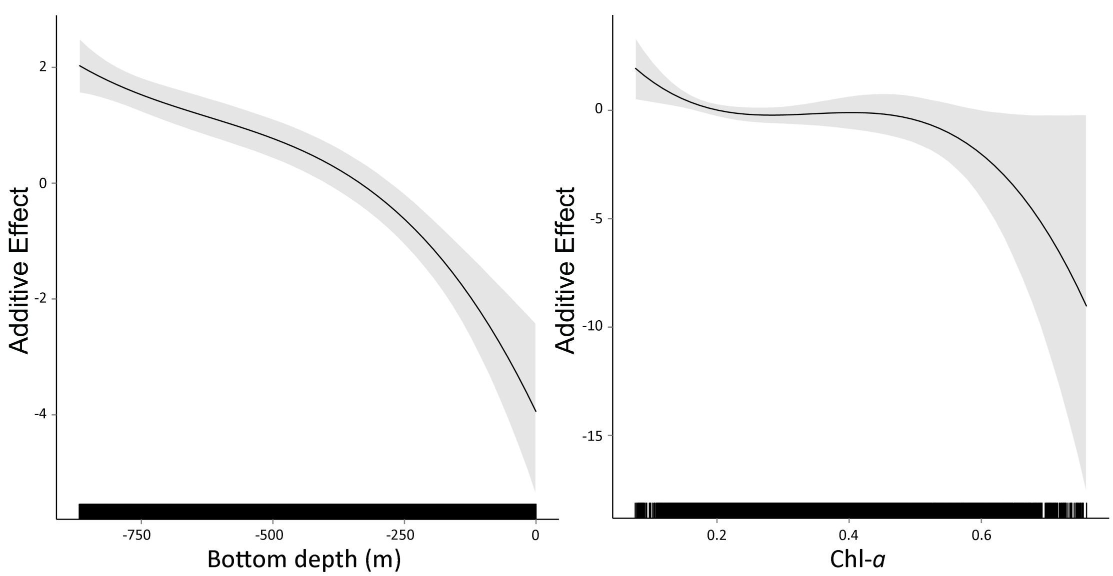

Figure 15. Response curves of the relationship between striped dolphin occurrence and bottom depth (left), and between striped dolphin occurrence and Chl-*a* concentration (right). Zero on the vertical axis corresponds to no effect of the covariate on the estimated response. Positive values on the vertical axis correspond to a positive relationship between the covariate and occurrence of dolphins, while negative values correspond to a negative relationship. Shaded areas represent 95%CI as calculated by GEE.

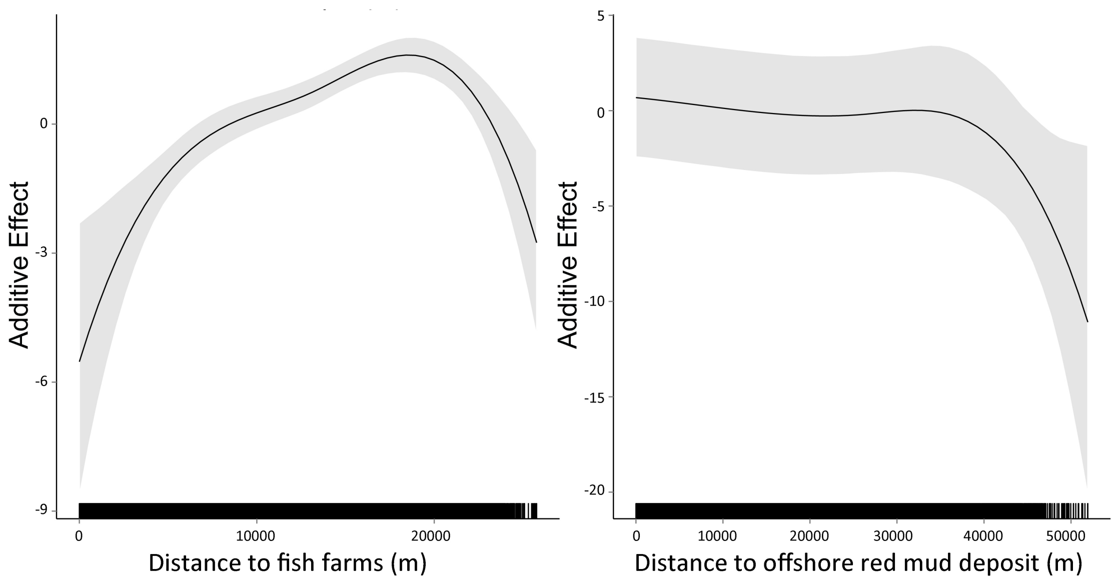

Figure 16. Response curves of the relationship between striped dolphin occurrence and distance to fish farms (left), and between striped dolphin occurrence and distance to offshore red mud deposit (right). Zero on the vertical axis corresponds to no effect of the covariate on the estimated response. Positive values on the vertical axis correspond to a positive relationship between the covariate and occurrence of dolphins, while negative values correspond to a negative relationship. Shaded areas represent 95%CI as calculated by GEE.

DISCUSSION

This study rejected the null hypothesis a random distribution within the Gulf of Corinth, and showed clear habitat preferences for both bottlenose and striped dolphins, with additional evidence of habitat partitioning between the two species. Bottlenose and striped dolphin habitat use was generally consistent with patterns observed in other Mediterranean areas, especially in terms of bottom depth, with an apparent affinity for waters shallower and deeper than 300 m, respectively. However, some findings in this study tend to contrast with observations in other areas, and some are specific to the Gulf of Corinth. Below, I summarize and discuss the main results for each of the two species. Additionally, I identify some shortcomings of this study, suggest priorities for future research, and frame my results in the context of ongoing conservation management efforts.

Bottlenose dolphins

In the Gulf of Corinth, bottlenose dolphins were mainly encountered and followed along the northern coast, a distribution preference that was also supported by the geographical submodel indicating a drop of occurrence at latitudes less than 38.2°N. Such geographic preference may have implications in terms of interactions with local fisheries. A parallel study on the impact of dolphin depredation on the small-scale fishery found that fishers operating in the northern section of the Gulf of Corinth suffer a significantly greater damage (in terms of perceived economic loss) than those operating in the southern sector (Bonizzoni et al. 2016). Gear damage and depredation in the Gulf are most likely caused by bottlenose dolphins (and to a lesser extent by loggerhead sea turtles *Caretta caretta*), consistent with fisher reports, as striped dolphins are not known to depredate fishing gear.

Modeled effect of longitude was weak, indicating an unimportant influence on bottlenose dolphin occurrence across the Gulf of Corinth. Mid-distance movements of individuals photo-identified within the Gulf to areas outside of the Gulf were reported by Bearzi et al. (2011b), indicating that at least some individuals travel extensively longitude-wise, and may exit the Gulf on opportunistic bases. However, scarcity of observations and group follows in the northeastern sector of the Gulf, possibly related to insufficient survey effort, call for additional field research effort.

As found in other Mediterranean areas (Cañadas et al. 2002, 2005; Cañadas and Hammond 2006; Gnone et al. 2011), bottlenose dolphins in the Gulf of Corinth prefer continental shelf waters and they seem to avoid deep waters. However, contrary to Cañadas et al. (2002) and Blasi and Boitani (2012), this study did not support a preference for steep bottom slopes. Bottlenose dolphins in the Gulf of Corinth occur in waters less than 300m deep, with either flat or gentle bottom slopes.

Neither SST nor Chl-*a* were found to affect bottlenose dolphin distribution in the Gulf. Distance to upwelling areas was the only environmental variable retained by the model. Bottlenose dolphin occurrence decreased in waters 40+ km away from productive areas; after this distance, however, confidence intervals were wide, suggesting this pattern must be treated with caution.

Proximity to fish farms had a strong impact on bottlenose dolphin distribution in the Gulf of Corinth. Dolphin occurrence was higher in waters within 10 km of farms, and peaked in their close proximity—particularly in the northern sector where virtually all fish farms are located (Figure 6). This finding is consistent with studies conducted in the Northern and Southern Evoikos Gulf (Bonizzoni et al. 2014, 2015), two other semi-enclosed areas in central Greece where bottlenose dolphins were described as "fish farm specialists" due to their strong preference for coastal fish farms. In the Northern Evoikos Gulf, bottlenose dolphin occurrence increased within 20 km of fish farms, and the animals preferred clusters of farms characterized by gently sloping bottom (Bonizzoni et al. 2014). In the Southern Evoikos Gulf, bottlenose dolphins spent 63% of their time within 1 km of fish farms, and 93% of the individuals photo-identified in this area were consistently observed foraging in close proximity to fish farm cages (Bonizzoni et al. 2015). Another study conducted in the Inner Ionian Sea Archipelago, Greece, found that occurrence of bottlenose dolphins increases in the proximity of fish farms, which were described as "a new trophic resource for bottlenose dolphins" (Piroddi et al. 2011). In the wider Mediterranean region, bottlenose dolphins have been observed foraging in the proximity of fish farm cages on a regular basis in eastern Sardinia, Italy (Díaz López 2006, 2012; Díaz López and Bernal Shirai 2007) and in the waters of Lampedusa, Italy (Pace et al. 2012). Indeed, fish farms have wide ecological effect on marine fauna (Karakassis et al. 2000; Machias et al. 2005; Dempster and Sanchez-Jerez 2008). Such influence, which can extend beyond the immediate vicinity of the cages (Machias et al. 2005; Weir and Grant 2005), is due to organic enrichment in the sediment (Karakassis et al. 1998), compositional and functional changes in benthic communities (Karakassis et al. 2000; Ruiz et al. 2001), and attraction of wild fish by providing structure and refuge from predators (Dempster et al. 2002). Consistent with findings in other areas, fish farms areas in the Gulf of Corinth likely represent important feeding spots for bottlenose dolphins as they travel from one facility to the next in search of prey. The present study documented local fishers often setting their nets in the proximity of fish farms, where catches reportedly tended to be higher, supporting the hypothesis of a higher local abundance of fish, which may be advantageous to both bottlenose dolphins and local fishers using bottom-set nets.

The coastal red mud deposit was not retained by the model for bottlenose dolphins. Such apparent lack of avoidance would imply potential exposure to red mud. Of the total tracked movements of this species, 11% occurred in waters above the red mud deposit, and on one occasion bottlenose dolphins in the Bay of Antikyra were observed surfacing covered by red mud. Bottlenose dolphins are known to occur in Mediterranean areas heavily impacted by human activities as long as prey is available (Bearzi et al. 2008c; Bonizzoni et al. 2014). Bottlenose dolphins are primarily bottom feeders, and thus any use of the red mud area could result in both direct and indirect exposure to toxic contaminants, with unknown but potentially relevant health effects, e.g. via the food web (Desforges et al. 2016; Jepson et al. 2016).

Striped dolphins

Striped dolphins occurred mainly in the deep central and southern sectors of the Gulf of Corinth, as shown by the response to latitude. While longitude was also retained, the apparent slight increase in striped dolphin occurrence in the western quarter of the Gulf has wide confidence intervals and is likely a spurious result. During the 5 years of this study there were actually no observations west of 22° 08' 30"E. Additionally, since 1991 no striped dolphin sightings were ever reported in the western quarter of the Gulf (Frantzis et al. 2003). Striped dolphin absence in the western sector are consistent with the hypothesis that striped dolphins do not travel in and out of the Gulf, but instead constitute a geographically isolated population (Frantzis et al. 2003; Frantzis 2009; Bearzi et al. 2011a, in review). The physiography of the Gulf of Corinth probably plays a role: western waters are less than 400 m deep, with a maximum depth of only 65 m under the Rion-Antirion bridge (Figure 1). West of the bridge, the Gulf of Corinth is separated from deep Ionian Sea waters by the shallow continental shelves of the Gulf of Patras and Prokolpos Patron. This vast area of waters less than 50-100 m deep may represent an unfavorable habitat for a pelagic species such as the striped dolphin, and limit immigration/emigration. The striped dolphin isolation hypothesis (Frantzis 2009) is further supported by genetic studies showing that striped dolphins sampled in the Gulf of Corinth differ from individuals sampled in the Ionian Sea and other Mediterranean areas (Gkafas et al. 2007; Gkafas 2011).

Distance from shore and bottom slope do not seem to affect the distribution of striped dolphins in the Gulf, consistent with findings in the Ligurian Sea (Azzellino et al. 2008). Conversely, distribution modeling showed a marked preference for deep waters. Model output indicated that striped dolphin occurrence increases with increasing depths, and waters less than 300 m deep were generally avoided (Figure 12, left). A strong preference for deep waters was also apparent in other Mediterranean areas (Cañadas et al. 2002; Gannier 2005; Azzellino et al. 2008; Panigada et al. 2008). While striped dolphins have rather opportunistic feeding habits, they typically target epi- and meso-pelagic prey (Würtz and Marrale 1991; Spitz et al. 2006; Öztürk et al. 2007; Scuderi et al. 2011; Dede et al. 2015).

SST and upwelling areas were not retained by the models and they did not seem to represent important factors affecting striped dolphin distribution, consistent with other Mediterranean studies (Cañadas et al. 2002; Azzellino et al. 2008). Chl-*a* concentration showed a negative effect, with higher occurrence of striped dolphins in areas with low Chl-*a* values—a pattern also observed in the Ligurian Sea (Laran and Druout-Dulau 2007; Panigada et al. 2008) and in the Bay of Biscay and English Channel (Hobbs 2004). However, in this study, the finding might be an indirect effect of striped dolphin preference for the deepest portions of the Gulf, as offshore waters are generally characterized by lower chlorophyll concentrations (Griffin and Griffin 2003).

The influence of fish farms on striped dolphin distribution has never been investigated. In the Gulf of Corinth, dolphin occurrence was higher at distances between 10 and 22 km from the cages, while their occurrence dropped outside of this range. This result likely reflects the striped dolphins' preference for deep waters away from the coast where fish farms are located rather than a direct effect of farming (Figure 16). However, a potential causation cannot be ruled out considering that striped dolphins prefer oligotrophic waters and fish farms are known to contribute to high nutrient loads (Dempster et al. 2002; Machias et al. 2005).

Distribution modeling did not indicate avoidance of the offshore red mud deposit by striped dolphins, as is also suggested by their tracked movement patterns (Figure 10). Boat follows yielded 654 km of striped dolphin movements over red mud deposits: 35% of the total. Because the red mud affects predominantly the seafloor and benthic organisms, direct impacts on striped dolphins (that are predominantly epi- and meso-pelagic feeders) would not be expected. However, food-web effects and biomagnification of contaminants may occur and overlap between striped dolphin habitat and red mud deposits raises concern, considering the immunotoxic and other detrimental effects of environmental pollutants (Desforges et al. 2016; Jepson et al. 2016). The modeled decreased occurrence away from the offshore red mud deposit likely reflects the striped dolphins' strong affinity for the deeper portion of the Gulf where the red mud naturally deposits as sediment.

Methodological considerations

A key explanatory variable that is often missing in habitat modeling studies is prey distribution. To overcome in part the problem of poor or absent information on prey density and distribution (often hard to obtain or measure), abiotic variables such as Chl-*a* are often used as proxies of primary production (Cañadas and Hammond 2006). Such proxies, however, are unlikely to have a direct influence on habitat selection by high-order predators such as dolphins (Torres et al. 2008). Additionally, the relationship between dolphin distribution and dynamic ecological variables such as SST, Chl-*a* and upwelling areas may not be directly related at the time of observations, because Chl-*a* peaks are temporally separated from zooplankton peaks, which in turn may influence the occurrence of dolphin prey. As a result, Chl-*a* peaks may be separated in time from predator concentrations (Panigada et al. 2008). Future research in the Gulf of Corinth should explore whether dolphin distribution is affected by oceanographic variables such as SST and Chl-*a* by incorporating *delayed* responses to these variables. For instance, creating lagged covariates (e.g. with one, two, and three month lags) would allow to assess whether dolphins show delayed responses to such variables.

Anthropogenic impacts and conservation aspects

Despite the considerable amount of red mud discarded into the Gulf over several decades, no information is available on potential effects on dolphins and other high-order predators. Dumping of red mud has known detrimental effects on marine life (Rosenthal 1971; Paffenhoefer 1972; Dethlefsen and Rosental 1973). Red mud dumping can increase water turbidity (Power et al. 2011) and heavy metal concentrations (Iatrou et al. 2010a,b). PCBs and DDTs concentrations in the Bay of Antikyra were among the highest recorded in the coastal waters of Greece (Tsangaris et al. 2011). Botsou and Hatzianestis (2012) reported high contaminant levels of polycyclic aromatic hydrocarbons (PAHs) in sediments collected near the aluminum plant, and high levels of metals were found in seagrass *Posidonia oceanica* from the Bay of Antikyra (Malea et al. 1994). Distribution modelling in the Gulf of Corinth yielded no strong correlation between red mud deposits and dolphin occurrence, suggesting that dolphins are unlikely to avoid those areas. A high degree of overlap was apparent between the location of red mud deposits and critical habitat of both bottlenose and striped dolphins. Such overlap raises concern, considering the immunotoxic and other detrimental effects of environmental pollutants

(Desforges et al. 2016; Jepson et al. 2016). Future research should investigate the potential effects of decades of red mud dumping on the Gulf's food webs, including high-order predators such as dolphins.

Lack of information and historical baseline data prevent understanding of the past and present impacts of fishing (including depletion of dolphin prey) in the Gulf of Corinth. A parallel investigation conducted during this study (S. Bonizzoni and G. Bearzi, unpublished data) showed that a small-scale fishing fleet including approximately 300 active boats of 5–12 m operates in the Gulf of Corinth. Additionally, the Gulf is exploited by an intermediate-scale industrial fleet of approximately 10–15 bottom trawlers and purse seiners of 15–25 m. Current fishing regulations in the Gulf include a ban on bottom trawling between April and November, and a ban of purse seining within 300 m from the coast and in waters less than 50 m deep (Vassilopoulou et al. 2012). Beach seining, a fishing method banned throughout Europe, was recently restricted to waters deeper than 50 m (a measure that makes this kind of fishing largely ineffective). However, regulations are insufficiently enforced and illegal fishing by purse and beach seiners was observed during this study. An interview survey conducted in 2013 (S. Bonizzoni and G. Bearzi, unpublished data) investigated the threats perceived by local fishers as having an impact on fish stocks and landings in the Gulf of Corinth. Of 104 fishers interviewed, 46 (44%) reported beach seiners, purse seiners, bottom trawlers, or overfishing in general as negatively influencing their catch. Overall, seiners and trawlers were perceived by fishers as the main anthropogenic factor threatening fishing viability in the Gulf (also see Bearzi et al. 2008b, 2010). Future studies should consider an appropriate assessment of the year-round industrial fishing effort and landings. Additional attention should be devoted to investigating instances of illegal fishing and occurrence of incidental mortality in fishing gear of dolphins, sea turtles and other protected species. Ecosystem modelling would be a valuable tool to investigate trophic interactions and fisheries-related ecological perturbations in the Gulf of Corinth, as it was successfully done in other areas of Greece (Piroddi et al. 2010, 2011).

Cetaceans and marine life can be threatened by underwater noise and disturbance (Nowacek et al. 2007; Würsig and Richardson 2009). The Gulf of Corinth is an area of great interest for geophysical research and seismic surveys producing intensive noise are not infrequent (Taylor et al. 2011; Beckers et al. 2015). Furthermore, during this study motor yachts were sometimes observed crossing dolphin groups at high speeds. Management measures to protect dolphins should include regulations to reduce noise and direct disturbance, which may also prevent boat collisions. High-speed sport competitions overlapping dolphin habitat (such as the jet-ski race organized in the Gulf of Corinth in 2013; www.hjsba.gr, www.jetraidgreece.com) imply high risks of collision and disturbance.

Conservation efforts in the Gulf of Corinth

All the marine mammal species known to occur in the Gulf of Corinth (bottlenose dolphin, striped dolphin, short-beaked common dolphin, Risso's dolphin and Mediterranean monk seal; Frantzis and Herzing 2002; Azzolin et al. 2010; Bearzi et al. 2011a, in review) are included in the EU Habitats Directive and protected by the national legislation of Greece. While there have been a number of calls for marine conservation in this area, no direct measures have been taken to ensure marine mammal protection.

In 2007, Greenpeace proposed the creation of a marine reserve in the Gulf (Greenpeace 2007). This proposal identified three core areas where different levels of human impact were allowed, with full protection granted to the eastern and western sectors of the Gulf (Figure 17). The Agreement on the Conservation of Cetaceans of the Black Sea, Mediterranean Sea and Contiguous Atlantic Area (ACCOBAMS), included the Gulf of Corinth among the "areas of special importance for the common dolphin and other cetaceans" and proposed the creation of a marine protected area (Resolution 3.22; ACCOBAMS 2007). The "National Strategy and Action Plan for the Conservation of Cetaceans in Greece" also granted high conservation importance to the Gulf (Notarbartolo di Sciara and Bearzi 2010; Figure 18). More recently, the Gulf of Corinth has been included in a EU-funded project (Monitoring and Evaluation of Spatially Managed Areas, MESMA) that identified several candidate zones for marine conservation within the Gulf (Giakoumi et al. 2012; Vassilopoulou et al. 2012; Stelzenmüller et al. 2013; Figure 19). Candidate "priority areas" for conservation have been evaluated according to the requirements of the EU Habitats Directive, and they were selected based on minimizing conflicts with economic activities such as fishing and tourism.

Figure 17. Zoning proposed by Greenpeace for the creation of a marine reserve in the Gulf of Corinth (from Greenpeace 2007; © Greenpeace). Full protection (no-fishing and no-human interference) was advocated in areas labeled with number 1.

Figure 18. Areas of special conservation importance (green), and areas of potential conservation importance (light green ovals) for cetaceans in the waters of Greece (from Notarbartolo di Sciara and Bearzi 2010; © Giuseppe Notarbartolo di Sciara and Giovanni Bearzi).

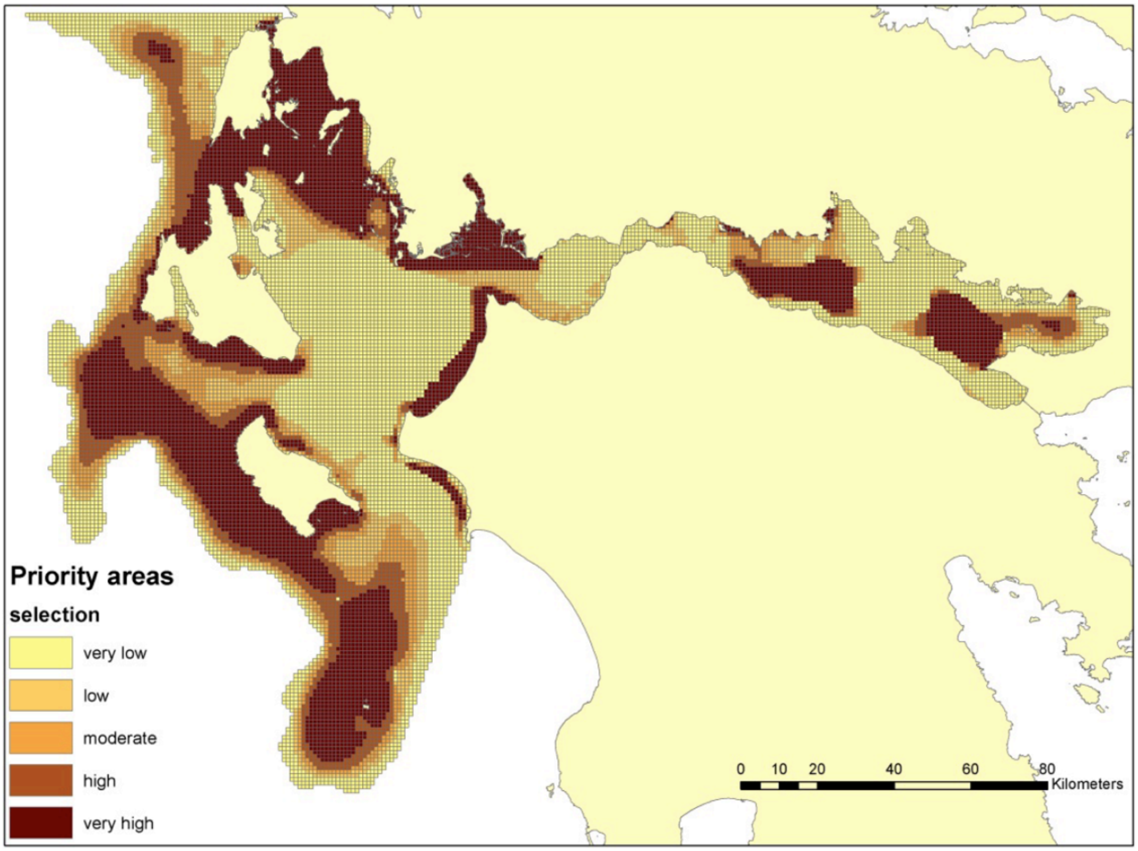

Figure 19. Suggested priority areas (very low to very high priority) for marine conservation in the Gulf of Corinth and adjacent Ionian Sea waters, based on a scenario intended to ensure high conservation levels (adapted from © Vassilopoulou et al. 2012).

CONCLUSIONS

Information contributed by this thesis can help improve marine spatial planning. Though proposals to manage the Gulf of Corinth and the surrounding Ionian Sea waters have been praiseworthy, so far inappropriate consideration has been given to dolphin abundance, status, and critical habitat within the Gulf. For instance, full protection proposed by Greenpeace to the eastern and western sectors of the Gulf has clearly become obsolete if one considers the information provided here, documenting the importance of the central deep-water portion of the Gulf for striped dolphins, as well as the importance of the northern continental shelf and of fish farm areas for bottlenose dolphins. Spatial management planning proposals have overlooked key information on dolphin abundance, status and distribution—largely because such information was unavailable at the time the proposals were made—and therefore failed to address important ecological aspects. These aspects include the degree of geographic isolation of striped and short-beaked common dolphins, making these subpopulations especially vulnerable to human impacts (Bearzi et al. 2016, in review). Anthropogenic impacts likely to have conservation relevance include the effects of fish farming, industrial fishing (particularly by purse seiners and bottom trawlers), and the massive dumping of industrial byproducts. Management of these and other impacts should take into account dolphin distribution, movements and critical habitat needs. This thesis pinpoints some of the geographic, bathymetric, environmental and anthropogenic factors likely to influence the distribution and habitat use of bottlenose and striped dolphins, also identifying important research gaps. Future management planning should take into account new information provided here (as well as data on abundance and trends contributed by recent studies conducted in parallel), to identify management measures that can ensure effective protection of vulnerable dolphin populations in a semi-enclosed inland basin.

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